United States
Department of
Agriculture

**Agricultural
Research
Service**

ARS-28

April 1985

Genetic Methods For the Control of Lepidopteran Species

Status and Potential

ABSTRACT

LaChance, Leo E. 1985. Genetic Methods for the Control of Lepidopteran Species: Status and Potential. U.S. Department of Agriculture, Agricultural Research Service, ARS-28,40 p.

Lepidopteran species are widely recognized as the most important pests of many major crops, forests, and stored products. Three genetic control methods that have been developed and field tested against Lepidopteran pests are the sterile insect technique, inherited sterility, and backcross sterility. This report presents the principles, advantages, and disadvantages of each of these methods and the potential of using the methods against Lepidopteran pests.

KEYWORDS: Autocidal control, backcross sterility, genetic control, hybrid sterility, inherited sterility, integrated pest management, Lepidopteran species, partial sterility, quarantine method

Copies of this publication may be purchased from the following: National Technical Information Service
5285 Port Royal Road
Springfield, VA 22161

ARS has no additional copies for free distribution.

CONTENTS

Genetic Methods for the Control of Lepidopteran Species

Status and Potential

By Leo E. LaChance [1] [2]

INTRODUCTION

During the past 25 years genetic methods for the suppression or eradication of insect pests have become a reality. Genetic pest suppression is unique among biological control methods in that it involves the release of genetically modified insects to control the same species; thus, these methods are autocidal. The best known, and a well accepted, autocidal control method is the sterile insect technique (SIT). Compared with chemical control methods, genetic methods are unparalleled in specificity and safety because only one species in the ecosystem is affected and virtually no chemicals are used. Although genetic methods are applicable to any sexually reproducing insect species, most major SIT programs have involved Dipteran species. To many entomologists, SIT and screwworms are almost synonymous.

Much has been written concerning the use of SIT to eradicate the primary screwworm, Cochliomyia hominivorax (Coquerel), from North America. The first major use of SIT was for the eradication of this species from the island of Curacao in 1954 (Baumhover et al. 1955). The pest was then eradicated from the Southeastern United States in 1959 and from the island of Puerto Rico in 1975 (Whitten 1982). A considerably more ambitious program was initiated in 1962. Its aim was to eradicate the screwworm fly from the Southwestern United States and to suppress the fly in northern Mexico. This program has been eminently successful. Less than a dozen screwworm infestations have been reported in the United States during the past 4 years, and none were reported in 1983 and 1984. Thus, screwworms have been eradicated from the United States, Baja CA, and much of Mexico north of the 20th parallel. The present goal of this joint Mexican-American program is to establish and maintain a barrier of sterile flies across the Isthmus of Tehuantepec in Mexico by 1985. Judging from the recent progress in the program, this is certainly an attainable goal.

---

[1] Research Geneticist and National Technical Advisor for Insect Genetics, Metabolism and Radiation Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, PO Box 5674, Fargo, ND 58105.

[2] Written, in part, while the author was on temporary assignment (24 October-11 November 1983) as a consultant to the Joint FAO/IAEA Division of Isotope and Radiation Applications of Atomic Energy for Food and Agricultural Development, Vienna, Austria.

The Mediterranean fruit fly, Ceratitis capitata (Wied.), is also a prime candidate for control by SIT. One of the leading organizations promoting the use of SIT for medfly control has been the joint Food and Agriculture Organization/International Atomic Energy Agency Division (FAO/IAEA). Under its leadership the SIT method for medfly suppression was originally tested in 1969 on the island of Capri in Italy. After the medfly was introduced into Costa Rica in the mid-1960's, an International Atomic Energy Agency/United Nations Development Program (IAEA/UNDP) project based in Costa Rica was initiated. The goal of this project was to test the feasibility of using SIT against medflies on a larger scale. It was planned to halt the northward movement of this important pest through Central America and eventually eliminate the pest north of the Panama Canal. Unfortunately, the program was abandoned in 1971, and, subsequently, the Mediterannean fruit fly spread throughout Central America. It was first detected in Mexico in January 1977 in the State of Chiapas adjoining Guatemala. With the assistance of both FAO/IAEA and the Regional Organization of Plant Protection and Animal Health and under an agreement with the U.S. Department of Agriculture, a major SIT program in Mexico was initiated. A mass-rearing facility was constructed in Tapachula, Mexico, in the State of Chiapas. The initial program goal was to stop the advance of the medflies north of Chiapas, Mexico, and eradicate the pest in Mexico and Guatemala; the long-term goal, to eliminate the pest from Central America. The medfly program in Mexico has been successful in that it has checked the movement of the pest north of the country, reduced the populations in the State of Chiapas to very low levels, and eradicated the pest from more than 3 million hectares in Mexico (Patton 1982). When the medfly was accidentally introduced into California in 1976 and again in 1980, SIT was an important component of an integrated pest management (IPM) program which succeeded in eradicating this pest from California. Currently, a program to eradicate the medfly from the Nile Delta and Valley in Egypt (2.5 million hectares) is being planned by Egypt and FAO/IAEA.

Although the medfly is not an important pest in the Far East, two other species of fruit flies are of considerable economic importance. These are the melon fly, Dacus cucurbitae, and the oriental fruit fly, Dacus dorsalis. Since there are no fruit flies in mainland Japan, the transport of untreated host fruits from infested areas is prohibited. Programs to eradicate these two species from several islands which lie south of Japan have been successful (Koyama 1982). These projects have utilized SIT in conjunction with other suppression techniques and have

greatly lessened the danger of importing fruit flies into Japan as well as increased export markets for these islands. In 1980, the Japanese Minister of Agriculture, Forestry and Fisheries and the prefectural government of Okinawa began a large-scale project to eradicate the melon fly from the whole of the Okinawa prefecture by utilizing SIT. This project involved the construction of a new facility to mass-produce 100 million melon fly pupae weekly (Kakinohana 1982).

In addition to the three major SIT programs discussed above, SIT has been developed to the point of commercial or large-scale implementation for onion flies, tsetse flies, and boll weevils; and there have been literally hundreds of smaller field tests and pilot experiments conducted to determine the usefulness of SIT for the suppression of other species. These include olive fruit flies, several mosquito species, stable flies, and horn flies. It is beyond the scope of this review to discuss all of these field programs in detail. Most of the information can be found in a series of FAO/IAEA publications (see references).

The remainder of this review will be devoted to an examination of autocidal control methods for Lepidopteran species. It is widely recognized that Lepidopteran species are the most important pests of many major crops, forests, and stored products. I will discuss methods that are currently available, the inherent advantages and disadvantages of each method, and the technical requirements for using autocidal methods against Lepidoptera. I also will examine in detail the potential of autocidal control for Lepidopteran species.

Three genetic control methods have been developed and field tested against Lepidopteran pests. These are the sterile insect technique (SIT), inherited sterility, and backcross sterility. Other genetic techniques currently being developed for Dipteran species (compound chromosomes, conditional lethal factors, chromosomal translocations and inversions) may eventually be applicable to Lepidopteran species, but will not be discussed herein.

The sterile insect technique for Lepidopteran species is identical to SIT for Dipteran species. It involves the mass-rearing of large numbers of insects, sterilization of males and females by ionizing radiation or chemosterilants, and their release to suppress the native population.

Inherited sterility (also known as inherited partial sterility, delayed sterility, or F_1 sterility) differs from SIT. For inherited sterility the radiation dose is lowered considerably so that the released insects (both males and females) are only partially sterile rather than completely sterile, or adjusted so that the females are completely sterile and the males partially sterile. The radiation dose can also be adjusted so that when the released partially sterile males and females interbreed, no progeny are produced but when they outcross with insects in nature, egg hatch is decreased and the progeny that are produced are sterile. The degree of sterility in the F_1 progeny is much higher than in the released insects, and significantly more male than female F_1 are produced.

Backcross sterility is currently available only for the suppression of *Heliothis virescens*. This approach involves the release of backcross insects derived from a cross of *H. subflexa* females with *H. virescens* males. The progeny from this cross consist of fertile females and sterile males. These fertile females attract and mate with *H. virescens* males either in the laboratory or in nature, and they continue to produce fertile daughters and sterile sons indefinitely.

ADVANTAGES AND DISADVANTAGES OF GENETIC CONTROL METHODS

Sterile Insect Technique

SIT has been extensively investigated for the control of Lepidopteran species, and the advantages are the same as for SIT in Dipteran species. A major drawback is that very high doses of radiation are required to fully sterilize Lepidopteran species. Radiation doses below 10 kilorads will sterilize the males of many Dipteran species, but doses of 30 to 50 kilorads are often required to sterilize males of Lepidopteran species (LaChance et al. 1967, North 1975). These high radiation doses very often reduce competitiveness. Reduced competitiveness can be due to a shortened lifespan, lack of dispersion of the released insects, or loss of synchrony in biological rhythms. Other changes in Lepidopteran species induced by high radiation doses are reduced ability to transfer spermatophores, decreased sexual activity, increased mating times, and decreased longevity of sperm (White et al. 1975, Souka et al. 1975, Hutt and White 1974, Sokolowski and Ski 1980, Van Steenwyck et al. 1979). Another cause of decreased competitiveness in some species is a decreased ability of the males to inseminate the females with eupyrene sperm. Such a species is the cabbage looper (Holt and North 1970, North and Holt 1971) but not the codling moth or H. zea (North and Holt 1971, White et al. 1975). When eupyrene sperm are not transferred to females, they will remate and are reluctant to initiate oviposition. Also, since the released insects are fully sterile, suppression of the native population ends whenever the release of sterile insects ceases.

Inherited Sterility

North (1975) listed 14 species of Lepidoptera in which inherited sterility had been demonstrated. Several additional species have since been added: European corn borer, Ostrinia nubilalis (Huebner), (He-qin and Hong-shang 1980, Nabors and Pless 1981); fall armyworm, Spodoptera frugiperda (J. E. Smith), (Carpenter et al. 1983); almond moth, Cadra cautella (Walker), (Brower and Tilton 1975); and silkworm, Bombyx mori, (Sugai and Mirumachi 1973, Murakami 1976), to mention only a few. The major point is that we can expect inherited sterility to be induced in any Lepidopteran species as well as in some Hemipteran species. Further, inherited sterility in Lepidoptera has the same attributes in all species examined: F_1 males and females are more sterile than the P_1 males and females that are irradiated, and more F_1 male progeny than female progeny are produced. In some species, the F_1 progeny may develop more slowly than larvae from nonirradiated parents; and at some radiation doses, the F_1 males may mate but fail to inseminate females with eupyrene sperm.

The release of partially sterilized insects offers far greater suppressive potential than the release of fully sterile insects. Knipling (1970) was the first to recognize the potential of inherited sterility over SIT. In his initial models comparing the two approaches, he estimated that to achieve the same degree of suppression in a native population over three generations, four times as many sterile insects as partially sterile insects would have to be released. Similar conclusions of the superior suppressive potential of inherited sterility were expressed by North (1975) and by a number of authors in an IAEA symposium (North and Holt 1971). All theoretical models comparing inherited sterility with SIT have shown that partially sterilized insects suppress the native population more effectively than do an equal number of fully sterile insects.

The inherited sterility approach has numerous other advantages over SIT. Since lower radiation doses are used, the released insects should be more competitive. Several studies have shown that the released males have better sperm transfer ability (North and Holt 1970) and are more competitive (Charmillot et al. 1973, Brower 1979, 1982). Since the F_1 progeny are reared under field conditions, their biological rhythms should be in synchrony with those of the native insects.

The magnitudes of the immediate and delayed effects of inherited sterility can be varied by the dose of radiation used. Many species of Lepidoptera are partially sterilized by doses of 5 to 20 krad. Higher doses will increase the supressive effects of the released and F_1 generations. Lower doses will provide less immediate suppression but will affect more generations. The relative merits of high versus low doses of radiation in inherited sterility have been discussed by Knipling (1979, 1982) based on laboratory studies by Amoaka-Atta et al. (1978) and Brower (1980) on Ephestia cautella and others. These studies involved the irradiation of older pupae or adult males with doses of 0, 5, 10, 15, 20, and 30 krad and crossing the treated males with untreated females. The F_1 progeny were then inbred or outcrossed, and these crosses were continued for several generations. The number of possible crosses increases in each generation, and the results become more complex to follow. At the higher doses (15 or 20 krad), the researchers found the following to be generally true: When F_1 are inbred, the progeny are fully sterile; when the F_1 are outcrossed, high levels of sterility are found but the progeny lines that survive regain normal reproductive rates after only a few generations. Based on laboratory results,

Brower (1980) calculated the suppressive effects of a single release of various ratios of partially sterile males into a normal population. The results indicated that males receiving 15 and 20 krad had greater suppressive effects but by the third generation the population of partially sterile individuals was depleted leaving mostly descendants of native moths that would be fully fertile. In contrast, males treated with 5 and 10 krad had less suppressive impact in the released and F_1 generations but the effects persisted longer. Males treated with 10 krad reduced all three generations to a greater extent than 5 krad males.

Inherited sterility provides an opportunity to adjust immediate and delayed effects, depending on the needs of a particular program. In situations where a substantial number of F_1 progeny from released insects would be objectionable, it is possible to adjust the radiation dose so that no progeny will be produced when the released males and females mate and sterile progeny will be produced when the released insects outcross with native insects. By such an adjustment, the release of partially sterile insects should not augment the size of the natural population. If the situation permits the presence of a limited number of progeny from released insects (that is, when native insects are present in low densities), then the radiation dose can be lowered so that although some F_1 progeny will be produced when released insects inbreed or outcross, the suppressive effects of inherited sterility will persist for more generations. Thus, a considerable amount of fine tuning is possible with inherited sterility.

The genetic basis of F_1 sterility was elucidated by North and Holt (1968) and Bauer (1967) and has been reviewed by North (1975). When Dipteran species are irradiated, a high frequency of dominant lethal mutations are induced in the sperm and ova. In radio-resistant Lepidopteran species, dominant lethal mutations require much higher doses of radiation. When lower doses of radiation are administered, a high frequency of chromosome translocations are induced in the sperm and ova. The union of a translocation-bearing reproductive cell with a normal cell (from untreated moths) produces an F_1 that is heterozygous for one or more translocations. Heterozygosity for a single chromosome translocation produces individuals that are, on the average, 50 percent sterile. Moths heterozygous for more than one translocation are 75 to 100 percent sterile. Several cytological studies have demonstrated that F_1 progeny have multiple chromosome translocations (Bauer 1967, North and Holt 1968, North and Snow 1978, Ennis 1982). Thus, the suppressive effect of inherited sterility is expressed over

2 to 3 generations but is based on different genetic events in the first and second or third generations. The released P_1 moths have dominant lethal mutations in some of the sperm and ova and have chromosome translocations in the remaining sperm and ova. When outcrossed to native moths, gametes bearing dominant lethal mutations lead to the production of inviable zygotes whereas gametes bearing chromosome translocations allow the production of a reduced number of F_1 progeny that are totally or partially sterile, depending on the radiation dose administered to the released P_1 insects. If the F_1 progeny are totally sterile, then suppression of the population ends after the F_1 moths die. If the F_1 progeny are only partially sterile, then some of the F_2 progeny will also carry chromosome translocations and exert some degree of suppression. However, the frequency of chromosomally normal progeny increases each generation, since the insects with chromosome translocations produce fewer progeny than normal insects, and the suppression diminishes. For this reason, continued releases of partially sterile insects are required until the native population has been reduced to noneconomic levels.

Backcross Sterility

This genetic control method offers decided advantages over both SIT and inherited sterility. Unfortunately, it is presently available only for the suppression of one Lepidopteran species, Heliothis virescens. In comparison with SIT and inherited sterility, backcross sterility introduces sterility factors in the native population that can persist indefinitely. A number of theoretical models (Knipling 1979, Knipling and Klassen 1976) have shown that backcross sterility will exert a greater suppressive effect for a longer period of time than either SIT or inherited sterility. There are many reasons for this. First, the released males and females have received no radiation treatment. Second, in order to maintain the line, the backcross females are consistently backcrossed to H. virescens males. This leads to incorporation of virtually pure H. virescens genetic material into the line. For this reason, the released insects are expected to be behaviorally nearly identical to the H. virescens colony. Backcross females attract as many H. virescens males as native H. virescens females (Carpenter et al. 1979) and produce as many progeny.

Inherited sterility and backcross sterility also offer some degree of protection against the total collapse of a program due to short-term production failures in mass-rearing, because the suppressive effects persist for one or more generations.

One major disadvantage of the backcross sterility approach is that two strains of insects, the backcross (BC) line and the Heliothis virescens line, must be maintained separately. In each generation, BC females must be outcrossed to H. virescens males to perpetuate the line. This requires that the BC line must be kept totally pure and separate from the H. virescens line. Before the H. virescens males are introduced into cages with females from the BC line, every precaution must be taken to ensure that only H. virescens males are introduced. Sexing errors leading to the incorporation of H. virescens females would contaminate the BC line and could lead to the release of a few fertile H. virescens males and females. Use of BC sterility necessitates the highest standards of insect security to prevent contaminating the BC line with the fertile H. virescens line. Despite the need for sophisticated precautions which must be part of any backcross sterility program, and despite the applicability of the BC technique to only H. virescens at present, the potential of this approach is so impressive that it must be considered seriously. It is expected that continued research into the nature of hybrid sterility will produce other Lepidopteran species which exhibit hybrid or backcross sterility.

Unlike inherited sterility, the genetic basis for BC sterility is not fully understood. We do know that the sterile BC males produce abnormal eupyrene sperm and that the males do not inseminate the females (references in LaChance and Karpenko 1981, 1983). The nature of the sterility factor that is transmitted by the fertile females to the sons remains speculative. Possibly, a replicating cytoplasmic factor from the H. subflexa female ancestors interacts with the genetic material from the H. virescens line, causing abnormalities in sperm development.

Sterile Insect Technique

A SIT trial to suppress the corn earworm, Heliothis zea (Boddie), on the island of St. Croix, VI, was conducted in 1968-69 (Snow et al. 1971). Pupae reared in a facility at Tifton, GA, were shipped to St. Croix, and newly emerged adults were irradiated with 32 krad. The goal of releasing 6,000 males per day on the island was never achieved, however, and the results were somewhat discouraging. In those early days, mass-rearing of Lepidopteran insects had not been developed to the sophisticated levels possible today. There were serious drops in production, often resulting in periods when fewer than 1,100 males per day were produced. During such periods, very poor quality insects with high mortality and low fecundity were produced. Physiologically, the poor quality of the moths was shown by a high frequency of "locking" during mating of released males and native females. This exerts some degree of suppression expressed as a decrease in eggs oviposited rather than normal oviposition and decreased egg hatch expected in a SIT program. Further, H. zea males had poor quality sperm and often did not transfer eupyrene sperm during mating, or the sperm fragmented more easily (North et al. 1975).

The tobacco hornworm, Manduca sexta (L.), on St. Croix was suppressed during field trials during 1971-72 (Snow et al. 1976). In these experiments, the insects were reared on St. Croix and in Oxford, NC. A dose of 35 krad (95 percent male sterility) was given to pupae 2 to 3 days before adult eclosion. The size of the natural population was reduced by 93 percent, and there was a very close correlation between the percentage of nonhatching eggs collected in the field and the ratio of sterile to fertile males caught in traps. The correlation indicated that the released males were highly competitive.

Ironically, the largest program to date utilizing SIT against Lepidopteran species is not aimed at suppression or eradication; rather, it is used as a quarantine method to prevent the establishment of the pink bollworm, Pectinophora gossypiella (Saunders), in the San Joaquin Valley of California. This major pest of cotton entered the United States from Mexico in the early 1900's (Burrows et al. 1982); spread from Texas into New Mexico, Arizona, southern California, and northwest Mexico during the mid-1960's; and thus threatened the major cotton growing area in the San Joaquin Valley. In the Imperial Valley of California, where pink bollworms are established, the extremely high cost of control and level of damage (Burrows et al. 1982) fully justifies the SIT quarantine program in uninfested areas. Each year since 1968, sterile moths have been released in

the San Joaquin Valley (9 million in 1968, 772 million in 1982) (R. T. Staten, personal communication). The presence of sterile moths inhibits the reproduction of the relatively few moths or their progeny that do reach the valley by flight or other means. Pheromone traps are used for detection and monitoring. Although unmarked nonsterile moths have been trapped in the valley each season since 1967, the sterile released moths have prevented the establishment of this pest in the valley. In addition, the IPM program in this intensive agricultural area would be in serious jeopardy if routine insecticide applications were required for a key pest like the pink bollworm (Knipling 1982).

Although the release of sterile pink bollworms in the San Joaquin Valley has prevented the establishment of the pest, the feasibility of using SIT to control a large population of well established pink bollworms in an area had been evaluated only in relatively small field trials. These trials have been reviewed by Bartlett (1978).

A much larger field trial was conducted on the island of St. Croix from 28 December 1980 to 31 March 1982 (Henneberry and Keaveny 1984). In many respects, this trial was conducted under adverse conditions. The moths were reared in the USDA facility in Phoenix, AZ, (the same facility that produces sterile moths for the California program) and were irradiated as adults and shipped by air to St. Croix. A dose of 20 krad was used, and 50,000 to 100,000 sterile moths were shipped four times per week. Quality-control tests conducted on St. Croix showed that transit times of 20 to 26 hours resulted in 7 percent mortality; 40 to 56 hours, in 42 percent mortality; and longer than 56 hours, in 100 percent mortality. Because of shipment delays, there were 19 periods of 4 to 8 days when no moths were released in the test area.

Since the sterile males and females had been reared on an artificial diet containing red dye, it was possible to separate the released insects from the native ones caught in traps. By dissecting native females, it was also possible to determine whether they had mated with a released male (red spermatophore) or a native male (white spermatophore). This method introduces a bias in analyzing the results since released males do not transfer a red spermatophore at each mating after the first one. Also, when released females containing red dye are recaptured and examined it is difficult to determine whether they have mated with a released or native male. Furthermore, the strain used had been reared in factory conditions for more than 10 years and was probably laboratory adapted.

The results of the field trial have been analyzed in detail by Henneberry and Keaveny (1984). Briefly, it was possible to establish that all possible matings between released and native moths occurred but that there were more matings between native males and females than expected on the basis of trap catches. Mortality of the released moths was higher in the field than in the laboratory. Although more than 22 million moths were released during the experiment, the majority were caught less than 1 km from the release points and none were caught in traps 3 to 20 km. from the release points. Examination of cotton bolls revealed that fewer larvae were found than expected on the basis of prerelease and postrelease infestations, but ratios of at least 70 sterile moths to 1 native moth were required for suppression.

SIT has also been used to suppress the codling moth, Cydia pomonella (L.), (Wildbolz and Mani 1975). Proverbs (1982) summarized a variety of field tests conducted in Canada, the United States, and Europe. Suppression of the native population was achieved in virtually every field trial. Proverbs concluded, "The codling moth can be controlled very effectively by the SIT but current technology is not sufficiently advanced to permit economic implementation of the method at this time. Cheaper larval diets, better antimicrobial agents, and mechanization of rearing procedures would materially reduce the cost of insect production. Rearing at fluctuating temperatures and better method of quality control would result in a more competitive insect and in reduced cost of control." Of considerable interest is the finding of Proverbs et al. (1982) that when SIT was used to suppress codling moth populations, chemical sprays could be omitted for the next 2 years without any additional releases. Field experiments conducted in the U.S.S.R. and Switzerland (references in Proverbs 1982) have also shown the efficacy of SIT for codling moth suppression.

A number of SIT field trials to suppress other Lepidopteran pests have been conducted. These trials often involved comparisons of SIT with inherited sterility; and, for ease of presentation, they are discussed as a unit in the next section.

Inherited Sterility

Toba et al. (1972) conducted large cage tests comparing the suppression obtained from the release of fully sterilized (30 krad) and partially sterilized (15 krad) males of the cabbage looper, Trichoplusia ni. Greater suppression was obtained from a single release of partially sterile males (92 percent vs. 82 percent) over two generations. Thus, the results of theoretical models were validated in cage tests.

Partially sterilizing doses of radiation have also been shown to be more effective than fully sterilizing doses for the suppression of the codling moth. Proverbs et al. (1978) compared the effects of releasing moths treated with 25 krad (85 percent male and 100 percent female sterility) and 40 krad (98 percent male and 100 percent female sterility) in a large British Columbia orchard. After one season of releases, the wild population was reduced approximately 59 percent in the area with partially sterilized moths and 38 percent in the area with fully sterilized moths. Charmillot (1977) utilized much lower doses (10 krad, 60 percent male sterility) and released only males during the period of eclosion of the overwintered insects. Suppression of the native population was very good in the first generation and reasonably good in the second. Two-thirds of the F_1 male and one-half of the F_1 females recovered showed a high level of sterility.

Charmillot et al. (1976) conducted a field trial in which 10 krad males were mated to untreated females and the diapausing F_1 larvae (95 percent sterile) placed in artificial shelters in a small orchard. Emergence of the F_1 sterile moths was well synchronized with that of the wild population even though only one larval release was made in late winter and another in early July. No chemical sprays were needed against the codling moth, whereas in an adjacent orchard where no releases were made, two sprays were required each year.

Several field demonstrations on the use of autocidal methods to control the gypsy moth, Porthetria dispar (Linn.), have been conducted. Maksimovic (1974) reported on the earlier field trials in Yugoslavia. A series of field experiments have been conducted in the United States. All tests in the United States involved the release of males only because the sexes can easily be separated in the pupal stage. The first field test was initiated in 1978 near Benton Harbor, MI. Essentially, the population was detected in 1978 (one male trapped), delimited in 1979 (90 males trapped), and found to be an isolated population (approximately 1 square mile). In the spring of 1980, 110 larvae were detected. Based on larval distribution, an initial release strategy for sterile males was planned. Sterile males (15 krad, approximately 85 percent male sterility) were released during July in 1980, 1981 and 1982. Trap catches indicated that ratios of sterile to fertile (S:F) males were 14:1, 127:1 and 5,750:1 during the periods of adult male flight during these 3 years. The number of wild males caught during the 3 years decreased from 237 (1980) to 50 (1981) to 1 (1982) to none (1983) (Mastro and O'Dell, personal communication).

A field test of inherited sterility against gypsy moth was initiated in the summer of 1982 in Horry County, SC. The release of 10 krad males (60 percent sterility) began on 26 May and continued until 28 June. Approximately 9,000 males were released daily over 300 to 400 acres. Trap catches indicated that the S:F male ratio was 77:1. In 1982, 16 larvae and 13 wild males were recovered from the test area, while in 1983 only 5 males (either native or sterile F_1) were caught. Further monitoring of the area in 1984 will be required to determine whether the population was eliminated or is increasing (Mastro and O'Dell, personal communication).

Another test of the inherited sterility principle for gypsy moth suppression was recently initiated in a semi-isolated 100-acre wood lot in Maryland. During the summer of 1983, approximately 10,000 males per day were released. Trap catches indicated the ratio of 5 released to 1 native male was achieved during the period of peak flight activity. Monitoring of this area during the summers of 1984 and 1985 will be required to determine the effect on the native gypsy moth population (Mastro and O'Dell, personal communication).

In many respects, the gypsy moth is an ideal species for autocidal control. Because it is univoltine, releases are required only during a short period each summer. The females are flightless, and "sentinel" females can be placed throughout an area to attract either released or wild males. The sentinel females lay a large egg mass almost immediately after mating, and the egg masses can be recovered. However, since this species diapauses in the egg stage, an incubation period of about 6 months at low temperatures is needed before egg hatchability can be assessed. Egg diapause permits one interesting variation of the autocidal method. Males may be irradiated with substerilizing doses and mated with untreated females in the laboratory. The egg masses may then be collected, stored in diapause, and placed in infested areas in either the fall or the spring. The larvae emerging from these masses should be in synchrony with the native larvae, and the resulting sterile F_1 males and females would be expected to interbreed with the feral population and exert considerable suppressive effect. This novel variation of the inherited sterility method will be field tested in the United States in the near future, (Mastro and O'Dell, personal communication).

Backcross Sterility

H. virescens is a major pest in the United States. Protection of crops from this species is particularly difficult because H. virescens is resistant to many insecticides used against it but which instead destroy its

natural enemies. Therefore, it is considered a good candidate for genetic methods. A considerable amount of theoretical and applied research was conducted before the principle of backcross sterility was field tested. Based on the basic biological principles of Heliothis backcross sterility, Laster (1972), Laster et al. (1976), and Parvin et al. (1976) used theoretical models to estimate the effect of releasing backcross (BC) insects into native populations. They predicted that an isolated population of 1,000 native moths would decline to zero in 5, 9, or 19 generations following a single release of BC moths in a 30, 19, or 9 to 1 ratio of BC to native moths. In a further model, Makela and Huettel (1979) also predicted population suppression, but their model differed from previous models on the potential effect of moths migrating into the test area. All models stressed a most important factor: the ability to identify the BC from the native males trapped in the field trial. An equally important factor is the behavior of the BC insects as compared with that of the native insects.

First, it was important to determine the persistence of male sterility when BC females were backcrossed to H. virescens males. Laster et al. (1976) established that the pattern of male sterility and female fertility was maintained for over 40 generations. We now know that it persists for over 100 generations. Thus, we can be certain that if BC females attract and mate with H. virescens males in the field, then the sterility factor would be introduced and perpetuated in nature. Martin et al. (1981) showed that BC_8 insects enter physiological diapause, survive the winter, and emerge the following spring at the same time as native H. virescens. In laboratory cage tests (Laster et al. 1977, Pair et al. 1977), BC females did not differ significantly from H. virescens females in mating synchrony and frequency of mating with BC (sterile) and H. virescens (normal) males. However, when either type of female mated with BC males, it was more receptive to additional matings than females mated with H. virescens males. This is because the BC males do not transfer eupyrene sperm to the females during mating (Proshold and LaChance 1974; LaChance and Karpenko 1981, 1983). Later, Laster et al. (1978a) determined that traps baited with either H. virescens females or BC females were attractive to wild H. virescens males. Also, Raulston et al. (1979) reported that backcross females released in cotton at Brownsville, TX, were sexually attractive to native males; however, the released backcross males were noncompetitive in mating with native females. Carpenter et al. (1979) conducted experiments utilizing mating tables located in tobacco fields in Georgia. Mating tables

contained H. virescens and BC_5 females. They found that the H. virescens females attracted and mated with 162 native males and that the BC_5 females mated with 163 native males. A small variation in mating synchrony was observed. BC_5 females mated more frequently in the early evening hours and their mating activity peaked 1 hour before the mating peak for H. virescens females.

In field cage studies (Laster et al. 1978b), BC_3 and BC_6 were released along with H. virescens. The egg hatch was reduced through sterile matings, and the BC sterile trait was infused into the H. virescens populations.

Based on the encouraging preliminary studies, a pilot test was initiated in 1977 on St. Croix (218 square kilometers) to test the feasibility of the backcross sterility method against H. virescens (Proshold et al. 1982, 1983a, 1983b; Proshold 1984). The BC insects were reared at the USDA laboratory in Stoneville, MS, and shipped to St. Croix as pupae. During 1979 and 1980, BC_{12} and BC_{35} insects were released on the island. Each release period lasted from 4 weeks to 3.5 months. The method of release and the number of release sites varied considerably for the different tests. The number of insects released also varied--from 10,000 pupae per day (placed in emergence cages in the first two releases) to 40,000 pupae per day (in 50 release sites during the fourth release). In these tests, much information concerning the behavior of the BC and the native insects was accumulated (Proshold et al. 1983a, 1983b). Backcross females were observed actively flying, feeding, and mating earlier than native females; however, no difference in time of oviposition or preference for oviposition sites was detected. Activity time of the BC and the native males appeared to coincide. Mating interaction was random between native and backcross insects when BC insects were placed in the field as pupae and allowed to emerge. When adults were released, greater-than-expected mating among the released insects was observed, apparently due to inadequate dispersal of insects released as adults. Mating interaction between native and BC insects was verified by an increase in sterility of native females with increased numbers of released insects. Over the entire period, hatchability of eggs laid by native females (white eggs) decreased from 89 percent to 33 percent, whereas the hatchability of the eggs laid by the BC females (red eggs) was 83 percent after the first releases and dropped to 25.8 percent by the end of the fourth release period. During the fourth release period, only 25 percent of the native females captured were fertile. Of the released males captured, fewer than 15 percent were trapped farther than 1.6 km away

from the release site. Males placed in release cages as pupae dispersed farther than those released from a site as adults. However, eggs oviposited by released females were collected as far as 8 km from the release site, though most were collected near the release site. These data show the need for multiple release sites or aerial releases in future programs.

One of the most important findings of this study was random mating with native H. virescens when BC insects were released as pupae but not as adults. Infusion of the sterility factor into the native population was also demonstrated. After one generation of releases, one would expect to find unmarked native males that are the sterile progeny of BC females. Sterility of these trapped males can be assessed by mating them with normal females in the laboratory to determine if they transfer eupyrene sperm during mating or by cytological examination. During the longer fourth release period, the frequency of these sterile native males increased from 20 percent to 88 percent. Nearly 3 years after the release of BC insects stopped, sterile males were still being captured on St. Croix (Proshold, personal communication). Proshold et al. (1983b) concluded, "Whether the tobacco budworm can be suppressed by this technique in commercial agriculture is still to be determined. The results presented here indicate that the feasibility of Heliothis management by releasing hybrids will depend upon the number of native moths in the natural population and the cost of rearing and distributing the insects--not upon the behavior of the released insects or the interaction between the released and native insects."

The eventual application of BC sterility will depend largely on economic realities. Laster et al. (1976) calculated that in the Delta Area of Mississippi, insecticide treatments over 1.1 million acres would cost $21.7 million and that the release of BC insects over 4.6 million acres would cost $1.5 million. Knipling and Stadelbacher (1983) compared a variety of methods for areawide management of Heliothis populations. They estimated that genetic methods applied in the Delta Area of Mississippi would cost $3.3 million as compared with conventional control costs of $35 million and losses of $15 million.

All three genetic control methods for Lepidopteran species require basically the same information. Lists of these requirements have been compiled previously (Pal and LaChance 1974, Waterhouse et al. 1974) for genetic control programs. In the following section, I will attempt to stress certain aspects that have surfaced or changed during the past 10 years.

Mass-Rearing

When the book "Insect Colonization and Mass Production" (Smith 1966) appeared, only three species of insects could be reared "by the millions" and none were Lepidopteran species. Since then, progress in the mass-rearing of insects has been phenomenal; and many species of Diptera, Coleoptera, Hymenoptera and Lepidoptera have been reared in commercial quantities for pest suppression programs. Now, nearly 2,000 references describe methods for rearing 258 Lepidoptera, 204 Coleoptera, 138 Diptera, and 154 other species (Singh 1977). Scientists interested in insect mass-rearing exchange ideas and information regularly through an informal newsletter, "Frass." Doubtless, some Lepidopteran species are more difficult and more expensive to rear and are more susceptible to diseases during rearing than Dipteran species. Nevertheless, Leppla et al. (1982) list over 60 species of Lepidoptera which could easily be mass-reared and provides excellent guidance in plant design and sanitation principles. Another book, "Advances and Challenges in Insect Rearing," (King and Leppla 1984) provides additional expert guidance. Mechanization in mass-rearing can reduce the cost considerably. Sparks and Harrell (1976) were able to reduce the cost of rearing corn earworms from $13.61 to $5.81 per 1,000 pupae largely through mechanization. Techniques are now available for controlling the quality of the diet ingredients and for maintaining adequate sanitation--two of the most important factors in mass-rearing Lepidoptera. For a new species, certain existing methods may need to be modified; but sufficient information and expertise are available, so mass-rearing of Lepidoptera at a reasonable cost should not be an obstacle in a genetic control program.

Quality Control

A number of factors can affect the quality of laboratory-reared insects. Artificial diets are rather complex and tend to be nutritionally deficient. Laboratory strains can adapt to insectary conditions, and/or can undergo selection within colonies maintained over a long period. In doing so, they may show an alteration or loss of various rhythms that occur in feral insects. For example, we have presented several cases of colonization-induced changes in periodicity of mating or flight activity. If the laboratory colony deteriorates and is replaced by field

collected insects without proper precaution, diseases can be inadvertently introduced. All of these factors suggest that the quality of mass-reared Lepidoptera can often be suboptimal. However, high-quality insects can be produced. As in mass-rearing, there have been remarkable advances in quality control of mass-reared insects (Boller 1972, Boller and Chambers 1977a, 1977b; Bush and Neck 1976; Chambers 1977; Hoy 1976; Huettel 1976; Leppla et al. 1977, 1982; Leppla and Ashley 1978; McDonald 1976; Whitten 1980; King and Leppla 1984). The 1982 FAO/IAEA symposium "Sterile Insect Technique and Radiation in Insect Control" contains five papers on the quality control of mass-reared insects. An international working group on the quality control of mass-reared insects meets every 2 years (1982--Gainesville, FL; 1984--Wadenswill, Switzerland) under the auspices of the International Organization of Biological Control to exchange information and ideas. Therefore, a good many tools are available to detect even subtle changes in the quality of mass-reared insects.

Sterilizing Procedures

The literature contains numerous references on fully and partially sterilizing doses for a number of Lepidopteran species. These doses can serve as guidelines in the application of SIT or inherited sterility to a new species. Once the basic radiobiological information has been derived, continuing attention must be given so that the actual irradiation and handling operation does not reduce the quality of the product. Radiation doses should be kept to the minimum set by the goals of the program. Very often, the poor quality of insects is blamed on radiation damage when actually the damage was done during rearing and handling.

For backcross sterility to be used in controlling a species other than H. virescens, more extensive studies must be conducted to find two species which will hybridize and produce fertile female and sterile male progeny. Since members of the genus Heliothis include some of the most destructive plant pests and occur virtually worldwide, there are ample candidates for interspecific crossing studies. Actually, interspecific crosses may not be required. Possibly, the same species (subspecies?) from different continents (for example, H. armigera from Australia, Africa, or Europe) might be hybridized initially to determine the fertility of the progeny. If hybridization is not possible, then artificial insemination or in vitro fertilization techniques might be used.

Another approach is to utilize the techniques of molecular biology. The sterility of H. virescens and H. subflexa

hybrids and backcross progeny has been hypothesized (references in LaChance and Karpenko 1983) to be due to a cytoplasmic factor from the ancestral H. subflexa females that interacts with the H. virescens genes in BC males to produce sterility. If the hypothesis is correct, the identification, isolation, and transfer of this factor to another Heliothis species could result in hybrid sterility. It is important to realize that this transfer would probably be required only once and that, thereafter, the new strain could be maintained by backcrossing the fertile females to males of the parental strain.

Ecology, Dynamics, and Behavior

Before any genetic control method can be applied, the ecology, population dynamics, and behavior of the candidate species must be understood. This is absolutely critical. We must determine whether the species attacks a single host or several hosts and whether or not the alternate hosts are of economic importance. All hosts in the area capable of supporting the candidate species must be identified. Also needed are a reasonably accurate estimate of the absolute number of insects in the native population, information on how insect densities change over space and time, and information on when the native population is at the lowest level. If necessary, ancillary methods of reducing the natural population to minimal numbers may be required for genetic methods to be the most effective. Information on the rate at which the natural population increases during various seasons and the degree of immigration into the control area is vitally important. Equally important, in some crop ecosystems, is information on whether a particular crop has more than one major pest. If the use of genetic control on one key pest will lead to the better control of other pests by natural enemies, then the justification for the use is stronger than if pesticides were still required to control the other pests.

Distribution and Dispersal of Release Insects

Decisions concerning the best method of distributing the insects are intrinsically linked to information concerning the stage of the insects at irradiation (pupae or adults), the loss of competitiveness associated with handling and shipping and the degree of dispersal of the released insects. For example, the pink bollworm program in California uses a system wherein the adults emerge in the factory and are chilled, irradiated, and then transported in a chilled condition prior to aerial release. In the H. virescens trial on St. Croix, the insects were released as pupae or adults. The pupae were placed in emergence cages carefully protected from predators. Insects released as pupae dispersed farther than those released as adults (Proshold et al. 1983a). Similarly, gypsy moths are sexed,

and the male pupae are irradiated, transported, and placed in cages until they emerge as adults and disperse.

The distribution and dispersal system eventually adopted must be determined by field tests on the candidate species. It is of utmost importance that the entire control area receives good quality insects and that there be no blank spots, where few or no released insects occur. Also, when the density of the population varies in different areas, it may be necessary to vary the release rate so that certain areas receive more insects (hot spot treatments). Only preliminary research in the field can provide the information necessary for these decisions, and at times the system may involve certain compromises. Complete coverage of the release area may be obtained by the aerial release of adults that may be less competitive. Placement of pupae in ground emergence cages may be labor intensive but result in the release of adults that are in synchrony with the native population and more competitive. The degree of coverage achieved will depend largely on the degree of dispersal of the adults and the protection from predators.

Program Monitoring

The success of all genetic control programs ultimately depends on the ability of field personnel to monitor the progress of the program. In addition to releasing insects, an extensive system of traps baited with either synthetic pheromones (sex attractants) or virgin females must be deployed to lure both native and released males and establish the ratio of each in the area. When possible, eggs or egg masses deposited by females should be collected and hatchability determined. Also, recapture of native and released females followed by laboratory tests can establish the type of male they mated with (marked spermatophores), the number of matings, and egg hatchability. The importance of a good monitoring system cannot be overemphasized, and there are several pitfalls which should be kept in mind. I will mention only two.

The use of inherited sterility or backcross sterility can complicate monitoring because one generation after releases begin, we can expect to trap unmarked males that are the sterile progeny of released insects. Only laboratory tests of their fertility by mating to a normal fertile female or cytological examination of these males can determine whether they are the progeny of native males and females or of released and native insects.

Even when the released insects are "completely" sterile but massive numbers are released, certain possibilities must be

kept in mind. For example, in the California pink bollworm program a radiation dose of 20 krad was used which induced 99.9 percent sterility. However, in a large-scale laboratory test that used a sample of 720,000 irradiated insects, one normal appearing F_1 adult per 1,000 parent females was produced. Most of the F_1 had a high degree of adult deformities and high mortality in the immature stages. Also, the ratio of males to females was 2.2 to 1, and these progeny were sterile (Miller et al. 1984). Nevertheless, the authors calculated that during the years 1976 to 1981, when millions of irradiated moths were released, 2 to 17 percent of the insects recaptured and classified as native moths were probably sterile F_1 progeny of released parents.

The use of pheromones may be indispensible in a good monitoring program but certain problems may complicate the analysis of the data. For example, we now realize that some Lepidopteran species consist of one or more races that respond to different blends of the same pheromone (Klun et al. 1975, Rothschild 1975). Therefore, we cannot assume that a particular pheromone blend will be equally effective in all areas or that it will attract a random sample of the entire population. Only field experiments can indicate whether native and released males are equally attracted by a given trap bait.

Economic Analysis

Before a decision can be made to invest in genetic control of a species, an indepth analysis of the pest species, including damage estimates, costs of control, effectiveness, and ecological effects of alternative control methods is required. The advantages of various methods of insect control should be analyzed and compared over several years. As Knipling (1979) pointed out, reducing pest populations to very low levels may be difficult and costly by the use of chemicals or by a combination of several methods. But, once this is accomplished, maintaining management by genetic means each year may be more economical and effective and more acceptable from an ecological viewpoint than any other method.

Organizational Structure

The areawide application of a genetic control program requires an effective team of scientists and technicians. The organization must have an excellent communication system so that field results can be received daily by program officials. Often, changes in program operations, such as the distribution of insects, location of ground personnel and trap lines, and hot spotting of certain areas, must be implemented rapidly. Such rapid changes are impossible without proper delegation of authority and communication.

Separation of Sexes Prior to Release

The sexing of release insects is not necessary for any of the genetic control methods being considered for Lepidoptera and would not be useful in the case of backcross sterility because the fertile BC females are required to introduce the sterility factors into the native population. Because very little is known about the basic genetics of economically important Lepidopteran species, it is unlikely that genetic-sexing methods that have been developed for Dipteran species will be available soon for Lepidopteran species. Some obstacles are the large number of very small chromosomes in most Lepidopteran species and different sex-determining mechanisms. Until a concentrated effort on the genetics of Lepidopteran species is made, it is unlikely that genetic sexing for most of the economic species will be developed despite the huge savings that would accrue in mass-rearing operations.

When the males and females differ drastically in size (as in the gypsy moth) they can easily be separated by mechanical devices. Sexing provides the option of irradiating and releasing males only and returning the females to the brood colony or using them to produce parasites or pathogens which could be used concurrently with genetic methods to suppress the population.

Finally, it should be obvious that regardless of the advantages of one genetic method over another, inherited and backcross sterility programs are not easier to conduct than a SIT program. Although fewer insects may be required for the same degree of suppression, most program requirements will be equally demanding and complex.

CANDIDATE SPECIES FOR AUTOCIDAL CONTROL

Virtually any Lepidopteran species is a potential candiate for genetic control, but the requirements outlined above may prohibit the use of autocidal methods except for truly major insect problems or require the integration of autocidal methods with other suppression methods. Naturally, a particular pest becomes a better candidate as more of the information previously outlined becomes available. Although the identification of candidate species should be based on a good economic analysis, some pests are so economically important in certain areas of the world that it is difficult not to consider them as potential candidates. Examples of such pests are the pink bollworm in Egypt, India and South America; H. armigera in Africa, Europe, Russia, Far East, Middle East and Asia; Spodopteran species in South America and Africa; Diatraea saccharalis in South America; Laspeyresia pomonella in Europe and the Middle East; Chilo species in Africa and Asia; H. zea in Central and South America; and H. virescens and H. zea in North America.

CHANGING CONCEPTS OF PEST MANAGEMENT

During the past 25 years, concepts of pest management have been evolving but have not kept pace with nor fully utilized genetic control methods, which are rapidly developing. Technical developments in insect control are probably one or two decades ahead of a good understanding and acceptance of the manner in which new technology must be employed for maximum benefits. Currently, there is a major emphasis on organized areawide management of major pests versus field-to-field control. However, control measures are usually applied when the need is critical. Knipling (1982) pointed out, "The present IPM system is basically a defensive method relying on year-to-year and crop-to-crop control of pests as the need arises. Such a defensive system will tend to force growers or health officials to continue to rely on fast-acting insecticides to deal with the pests when they threaten a crop or create a health problem." This concept of pest management is probably the major reason why IPM programs seldom include genetic methods. Before genetic control methods become more commonly used, the concept of preventive entomology will have to become more widely accepted. Preventive entomology proposes the use of suppressive measures before pest density reaches economically damaging levels. Many alternative control methods--such as genetic manipulations; sex pheromones; and augmentation with slow-acting parasites, predators, or pathogens--or various combinations of those methods will not be as effective or practical after the pests have already reached damaging or threatening levels.

In addition, areawide preventive entomology requires a critical analysis of the possible long-range economic and ecological advantages of this approach, as compared with those of farm-to-farm management procedures. Depending on the biology of the pest or pest complex, ecosystemwide management based on preventive entomology can make effective use of various types of control techniques at strategic times and places.

In addition to SIT, inherited sterility and backcross sterility methods have been developed for the control of Lepidopteran pests. Tremendous advances in mass-rearing, quality control, and sex attractants, as well as considerable experience gained in field trials and commercial programs, indicate that it is now feasible to consider genetic control of Lepidoptera. What is needed now is a greater appreciation of the longer term benefits of ecosystemwide preventive entomology than of farm-to-farm suppressive measures employed after pests have reached damaging levels.

Pest management officials should not be awed by the complexity and scope of areawide management programs utilizing genetic methods, the integration of these methods with other techniques when required, and the organizational and operational problems that are involved. It is encouraging that entomologists in developed and developing countries are considering these approaches for the management of some of our major pests.

REFERENCES

Amoako-Atta, B., Denell, R.E. and Mills, R.B. 1978. Radiation-induced sterility in Ephestia cautella (Walker) (Lepidoptera: Pyralidae): recovery of fertility during five generations after gamma irradiation. J. Stored Prod. Res. 14:181-188.

Bartlett, A.C. 1978. Radiation-induced sterility in the pink bollworm. U.S. Dept. Agric., Agricultural Res. Serv., Agric. Reviews and Manuals, ARM-W-1, 25 p.

Bauer, H. 1967. Die kinetische organization der Lepidopteran-chromosomen. Chromosoma 22:102-125.

Baumhover, A.H., Graham, A.H., Bitter, B.A., and others 1955. Screwworm control through release of sterilized flies. J. Econ. Entomol. 48:462-466.

Boller, E. 1972. Behavioral aspects of mass-rearing insects. Entomophaga 17:9-25.

Boller, E.F., and Chambers, D.L., editors. 1977a. Quality control: an idea book for fruit fly workers. Bull. SROP, WPRS 1977/5, 168 p.

Boller, E.F., and Chambers, D.L. 1977b. Quality aspects of mass-reared insects. In R.L. Ridgway and S.B. Vinson, editors, Biological control by augmentation of natural enemies, 500 p. Plenum Press, NY.

Brower, John H. 1979. Sub-sterilizing irradiation of Plodia interpunctella males: effects of three filial generations. Ann. Entomol. Soc. Amer. 72:716-720.

Brower, John H. 1980. Inheritance of partial sterility in progeny of irradiated males of Ephestia cautella (Lepidoptera: Pyralidae) and its effect on theoretical population suppression. Can. Entomol. 112:131-140.

Brower, J.H. 1982. Mating competitiveness of irradiation sub-sterilized males of the tobacco moth, Ephestia cautella. J. Econ. Entomol. 75:454-457.

Brower, J.H., and Tilton, E.W. 1975. Potential for control of Cadra cautella (Walker) by release of fully or partially sterile males. Int. J. Appl. Rad. Isot. 26:720-725.

Burrows, T.M., Sevacherian, V., Browning, H. and Baritelle, J. 1982. History and cost of the pink bollworm (Lepidoptera: Gelechiidae) in the Imperial Valley. Bull. Entomol. Soc. Amer. 28:286-290.

Bush, G.L. and Neck, R.W. 1976. Ecological genetics of the screwworm fly, Cochliomyia hominivorax (Diptera: Calliphoridae) and its bearing on the quality control of mass-reared insects. Environ. Entomol. 5:821-826.

Carpenter, J.E., Sparks, A.N., and Raulston, J.R. 1979. Competitiveness of Heliothis hybrid vs. H. virescens females for H. virescens males in Georgia tobacco. J. Georgia Entomol. Soc. 14:65-69.

Carpenter, J.E., Young, J.R., Knipling, E.F. and Sparks, A.N. 1983. Fall armyworm (Lepidoptera: Noctuidae): inheritance of gamma-induced deleterious effects and potential for pest control. J. Econ. Entomol. 76:378-382.

Chambers, D.L. 1977. Quality control in mass-rearing. Ann. Rev. Entomol. 22:289-308.

Charmillot, P.J. 1977. Lutte autocide contre le carpocapse (Laspeyresia pomonella L.): 3. Lachers de papillons substeriles. Bull. Soc. Entomol. Suisse 50:203-212.

Charmillot, P.J., Fossati, A., and Stahl, J. 1973. Production de males sterile du carpocapse des pommes (Laspreyresia pomonella L.) descendant de parents substeriles et examen de leur competitivite en vue de la lutte autocide. Schweiz. Landw. Forschung 12:181-188.

Charmillot, P.J., Stahl, J., and Rosset, S. 1976. Lutte autocide contre le carpocapse (Laspeyresia pomonella L.). 2. Resultats de deux ans de lutte par depot en vergers de larves diapausantes steriles. Bull. Soc. Entomol. Suisse 49:173:184.

Ennis, T.J. 1982. The sterile male approach to the control of the spruce budworm. In Sterile insect technique and radiation in insect control: proceedings of a symposium, Neuherberg, 29 June to 3 July 1981. p. 389-393. IAEA, Vienna, Austria.

Henneberry, T.J., and Keaveny, D.F., III. 1984. Suppression of pink bollworm by sterile moth releases. U.S. Dept. Agric., Agric. Res. Serv. [rept.] [in press]

He-qin, Shang, and Hong-shang, Lo. 1980. The inherited sterility of the European corn borer (Ostrinia nubilalis (Huebner)). China Agric. Science 1:70-73.

Holt, G.G., and North, D.T. 1970. Effects of gamma irradiation on the mechanisms of sperm transfer in Trichoplusia ni. J. Insect Physiol. 16:2211-2222.

Hoy, M.A. 1976. Genetic improvement of insects: fact or fantasy. Environ. Entomol. 5:833-839.

Huettel, M.D. 1976. Monitoring the quality of laboratory-reared insects: a biological and behavioral perspective. Environ. Entomol. 5:807-814.

Hutt, R.B., and White, L.D. 1974. Codling moth: effects of 0 and 38 krad of gamma irradiation on the mating capacity of males. Environ. Entomol. 3:645-646.

Kakinohana, H. 1982. A plan to construct the new mass production facility for the melon fly, Dacus cucurbitae Coquillett, in Okinawa, Japan. In Sterile insect technique and radiation in insect control: proceedings of a symposium, Neuherberg, 29 June to 3 July 1981, p. 477-482. IAEA, Vienna, Austria.

King, E.G., and Leppla, N.D. 1984. Advances and challenges in insect rearing, U. S. Dept. Agric., Agric. Res. Serv. [rept.], 306 p.

Klun, J.A., and cooperators. 1975. Insect sex pheromones: intraspecific pheromonal variability of Ostrinia nubilalis in North America and Europe. Environ. Entomol. 4:891-894.

Knipling, E.F. 1970. Suppression of pest Lepidoptera by releasing partially sterile males: a theoretical appraisal. Bioscience 20:465-470.

Knipling, E.F. 1979. The basic principles of insect population suppression and management. U.S. Dept. Agric., Agric. Handbook 512, 659 p.

Knipling, E.F. 1982. Present status and future trends of the SIT approach to the control of arthropod pests. In Sterile insect technique and radiation in insect control: proceedings of a symposium, Neuherberg, 29 June to 3 July 1981, p. 3-23. IAEA, Vienna, Austria.

Knipling, E.F., and Klassen, W. 1976. Relative efficiency of various genetic mechanisms for suppression of insect populations. U.S. Dept. Agric. Tech. Bull. 1533, 56 p.

Knipling, E.F., and Stadelbacher, E. 1983. The rationale for areawide management of Heliothis (Lepidoptera: Noctuidae) populations. Bull. Entomol. Soc. Amer. 29(4): 29-37.

Koyama, J. 1982. The Japan and Taiwan projects on the control and/or eradication of fruit flies. In Sterile insect technique and radiation in insect control: proceedings of a symposium, Neuherberg, 29 June to 3 July 1981, p. 39-51. IAEA, Vienna, Austria.

LaChance, L.E., and Karpenko, C.P. 1981. Effect of seven antibiotics on the growth and reproduction of Heliothis subflexa x H. virescens interspecific hybrids and backcross males. Ann. Entomol. Soc. Amer. 74:493-497.

LaChance, L.E., and Karpenko, C.P. 1983. Hybrid sterility in Heliothis subflexa x H. virescens (Lepidoptera: Noctuidae) crosses: expression after injections with antiviral agents, heat shocks and rearing at extreme temperatures. Ann. Entomol. Soc. Amer. 76:104-109.

LaChance, L.E., Schmidt, C.H., and Bushland, R.C. 1967. Radiation induced sterilization. In W. W. Kilgore and R. L. Doutt, editors, Pest control, biological, physical and selected chemical methods, p. 147-196. Academic Press Inc., NY.

Laster, M.L. 1972. Interspecific hybridization of Heliothis virescens and H. subflexa. Environ. Entomol. 16:682-687.

Laster, M.L., Martin, D.F., and Pair, S.D. 1977. Mating incidence of male Heliothis virescens, hybrid and backcross males from H. subflexa and H. virescens crosses. Ann. Entomol. Soc. Amer. 70:293-295.

Laster, M.L., Martin, D.F., and Pair, S.D. 1978a. The attraction of wild Heliothis virescens males to sex pheromone traps baited with Heliothis virescens and backcross females. Environ. Entomol. 7:19-20.

Laster, M.L., Martin, D.F., Pair, S.D., and Furr, R.E. 1978b. Infusion of hybrid Heliothis male sterility into H. virescens populations in field cages. Environ. Entomol. 7:364-366.

Laster, M.L., Martin, D.F., and Parvin, D.W. Jr. 1976. Potential for suppressing tobacco budworm (Lepidoptera: Noctuidae) by genetic sterilization. Miss. Agric. and For. Sta. Tech. Bull. 82:9 p.

Leppla, N.C., and Ashley, T.R., editors, 1978. Facilities for insect research and production. U.S. Dept. Agric. Tech. Bull. 1576, 86 p.

Leppla, N.C., Chambers, D.L., and Boller, E.F. 1977. A proposed system for implementing quality control in a pest management program. In E.F. Boller and D.L. Chambers, editors, Quality control: an idea book for fruit fly workers. IOBC Bull. SROP, WRPS 1977/5, 168 p.

Leppla, N.C., Fisher, W.R., Rye, J.R., and Green, C.W. 1982. Lepidopteran mass-rearing. In Sterile insect technique and radiation in insect control: proceedings of a symposium, Neuherberg, 29 June to 3 July 1981, p. 122-133. IAEA, Vienna, Austria.

Makela, M.E., and Huettel, M.D. 1979. Model for genetic control of Heliothis virescens. Theor. Appl. Genet. 54:225-233.

Maksimovic, M. 1974. The effect of the release of gypsy moth cobalt-60 sterilized males in the park of Jelsa on the Island of Hvar, Yugoslavia. Agron. Glas. 36:493-502.

Martin, D.F., Laster, M.L., and Pair, S.D. 1981. Backcross progeny from interspecific hybrids of Heliothis subflexa x Heliothis virescens: physiological diapause, winter survival and infusion into natural H. virescens populations. Environ. Entomol. 10:197-200.

McDonald, I.C. 1976. Ecological genetics and the sampling of insect populations for laboratory colonization. Environ. Entomol. 5:815-820.

Miller, E., Staten, R.T., Jones, E., and Pozzi, J. 1984. Effect of 20 krad of gamma irradiation on pink bollworm and their F_1 progeny. J. Econ. Entomol. 77:304-307.

Murakami, A. 1976. Inherited embryonic lethality in progeny of irradiated silkworm, Bombyx mori. J. Rad. Res. 17:46-47.

Nabors, R.A., and Pless, C.D. 1981. Inherited sterility induced by gamma radiation in a laboratory population of the European corn borer, Ostrinia nubilalis. J. Econ. Entomol. 74:701-702.

North, D.T. 1975. Inherited sterility in Lepidoptera. Ann. Rev. Entomol. 20:167-182.

North, D.T., and Holt, G.G. 1968. Inherited sterility in progeny of irradiated cabbage loopers. J. Econ. Entomol. 61:928-931.

North, D.T., and Holt, G.G. 1970. Population control of Lepidoptera: the genetic and physiological basis. Manit. Entomol. 4:53-69.

North, D.T., and Holt, G.G. 1971. Radiation studies of sperm transfer in relation to competitiveness and oviposition in the cabbage looper and corn earworm. In Application of induced sterility for control of Lepidopterous populations, p. 87-97. IAEA, Vienna, Austria.

North, D.T., and Snow, J.W. 1978. Recovery of chromosome aberrations from natural populations of corn earworms and tobacco budworms subjected to daily releases of partially sterile moths. J. Econ. Entomol. 71:358-360.

North, D.T., Snow, J.W., Haile, D., and Proshold, F.I. 1975. Corn earworms: quality of sperm in sterile males released for population suppression on St. Croix Island. J. Econ. Entomol. 68:595-598.

Pair, S.D., Laster, M.L., and Martin, D.F. 1977. Hybrid sterility: mating dynamics of backcross progeny from crosses of Heliothis subflexa and H. virescens. Ann. Entomol. Soc. Amer. 70:665-668.

Pal, R., and LaChance, L.E. 1974. The operational feasibility of genetic methods for control of insects of medical and veterinary importance. Ann. Rev. Entomol. 19:269-291.

Parvin, D.W. Jr., Laster, M.L., and Martin, D.F. 1976. A computer program for simulating the theoretical suppression of the tobacco budworm by genetic sterilization. Miss. Agric. and For. Exp. Sta., Dept. Agric. Econ. Staff Papers Series, 18 p.

Patton, P. 1982. Programa contra la mosca del Mediterraneo en Mexico. In Sterile insect technique and radiation in insect control: proceedings of a symposium, Neuherberg, 29 June to 3 July 1981, p. 25-37. IAEA, Vienna, Austria.

Proshold, F.I. 1984. Infusion of sterility into a native population of tobacco budworms following the release of backcross insects. J. Econ. Entomol. [in press].

Proshold, F.I., and LaChance, L.E. 1974. Analysis of sterility in hybrids from interspecific crosses between Heliothis virescens and H. subflexa. Ann. Entomol. Soc. Amer. 67:445-449.

Proshold, F.I., Laster, M.L., Martin, D.F., and King, E.G. 1982. The potential for hybrid sterility in Heliothis management. Proceedings of the International Workshop on Heliothis Management, 1981, Pantacheru, India, p. 329-340. Int. Crops Res. Inst. for the Semi-Arid Tropics.

Proshold, F.I., Martin, D.F., Laster, M.L., and others. 1983a. Release of backcross insects on St. Croix to suppress the tobacco budworm (Lepidoptera: Noctuidae): methodology and dispersal of backcross insects. J. Econ. Entomol. 76:885-891.

Proshold, F.I., Raulston, J.R., Martin, D.F., and Laster, M.L. 1983b. Release of backcross insects on St. Croix to suppress the tobacco budworm (Lepidoptera: Noctuidae): behavior and interaction with native insects. J. Econ. Entomol. 76:626-631.

Proverbs, M.D. 1982. Sterile insect technique in codling moth control. In Sterile insect control and radiation in insect control: proceedings of a symposium, Neuherberg, 29 June to 3 July 1981, p. 85-99. IAEA, Vienna, Austria.

Proverbs, M.D., Newton, J.R., and Campbell, C.J. 1982. Codling moth: a pilot program of control by sterile insect release in British Columbia. Can. Entomol. 114:363-376.

Proverbs, M.D., Newton, J.R., and Logan, D.M. 1978. Suppression of codling moth, Laspeyresia pomonella (Lepidoptera: Olethreutidae) by release of sterile and partially sterile moths. Can. Entomol. 110:1095.

Raulston, J.R., Sparks, A.N., Lingren, P.D., and Martin, D.F. 1979. Mating interaction between native tobacco budworms and released backcross adults. Environ. Entomol. 8:349-353.

Rothschild, G.H.L. 1975. Attractants for monitoring Pectinophora scutigera and related species in Australia. Environ. Entomol. 4:983-985.

Singh, P. 1977. Artificial diets for insects, mites and spiders, 606 p. Plenum Press, NY.

Smith, C.N. 1966. Insect colonization and mass production, 618 p. Academic Press, NY, London.

Snow, J.W., Burton, R.L., Sparks, A.N., and Cantelo, W.W. 1971. Attempted eradication of the corn earworm from St. Croix, U.S. Virgin Islands. U.S. Dept. Agric. Prod. Res. Rept. 125.

Snow, J. W., Haile, D.G., Baumhover, A.H., and others. 1976. Control of the tobacco hornworm on St. Croix, U.S. Virgin Islands by the sterile male technique. U.S. Dept. Agric. ARS-S-98, 6 p.

Sokolowski, R.J., and Ski, Z.W. 1980. Mating ability and sperm competitiveness of radio-sterilized codling moths, Laspeyresia pomonella (Lepidoptera: Olethreutidae). Pol. Pismo Entomol. 50:463-472.

Souka, S., Guerra, A.A., Garcia, R.D., and others. 1975. Effect of irradiation with ^{60}Co on transfer and motility of sperm and on mating of the tobacco budworm. Fla. Entomol. 58:307-312.

Sparks, A.N., and Harrell, E.A. 1976. Corn earworm rearing mechanization. U.S. Dept. Agric. Tech. Bull. 1554, 11 p.

Sugai, E., and Mirumachi, M. 1973. Inherited sterility in progeny of irradiated male silkworm, Bombyx mori L. Japan. J. Genet. 48:329-335.

Toba, H.H., Kishaba, A.N., and North, D.T. 1972. Reduction of populations of caged cabbage loopers by release of irradiated males. J. Econ. Entomol. 65:408-411.

Van Steenwyk, R.A., Henneberry, T.J., Ballmer, G.R., and others. 1979. Mating competitiveness of laboratory-cultured and sterilized pink bollworms for use in a sterile moth release program. J. Econ. Entomol. 72:502-505.

Waterhouse, D.F., LaChance, L.E., and Whitten, M.J. 1974. Use of autocidal methods. In P. DeBach, P.S. Messenger, and C. B. Huffaker, editors, Theory and practice of biological control, p. 637-659. Academic Press, NY.

White, L.D., Proshold, F., Holt, G.G., and others. 1975. Codling moth: mating and sperm transfer in females paired with irradiated and unirradiated males. Ann. Ent. Soc. Amer. 68:859-862.

Whitten, C.J. 1980. Use of the isozyme technique to assess the quality of mass-reared sterile screwworm flies. Ann. Entomol. Soc. Amer. 73:7-10.

Whitten, C.J. 1982. The sterile insect technique in the control of the screwworm. In Sterile insect technique and radiation in insect control: proceedings of a symposium, Neuherberg, 29 June to 3 July 1981, p. 79-84. IAEA, Vienna, Austria.

Wildbolz, T., and Mani, E. 1975. The present status of the SIRM for codling moth. Z. Angew. Entomol. 77:359-362.